On the genus *Heteroschismoides* Ludbrook, 1960 (Scaphopoda: Gadilida: Entalinidae), with descriptions of two new species

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ABSTRACT

Heteroschismoides is a deep-sea genus characterized by shells being between 10 and 20 mm as adults, sculptured by 9 to 10 prominent primary ribs and a unique deep irregular apical fissure on dorsal side, considered until now to include a single species: Dentalium subterfissum Jeffreys, 1877. During revision of material from several expeditions carried out by the Museum National d'Histoire Naturelle, Paris, two new species were identified and are here described: *H. meridionalis* new species and *H* antipodes new species In addition, designation of the lectotype of *H. subterfissus* is proposed, as well as new records for this species in the northeastern Atlantic ocean are given. Heteroschismoides meridionalis new species is closely related to H. subterfissus, but the first has a smaller maximum diameter of shell and smaller apical aperture diameter. Heteroschismoides antipodes new species from Solomon Islands is smaller than other two species for both, shell length and fissure extension. The distance of point of maximum curvature from the apex in *H. antipodes* new species is located nearer to the apex than in H. meridionalis new species and H. subterfissus. The results here obtained considerably enlarge the geographical distribution of the genus and suggest a worldwide bathval and abyssal distribution for this genus.

Additional Keywords: Heteroschismoides subterfissus, Heteroschismoidinae, tusk shell, lectotype, new species, Brazil, Solomon Islands, deep-sea

INTRODUCTION

The genus *Heteroschismoides* was proposed by Ludbrook in 1960 to include the deep sea species *Dentalium* subterfissum Jeffreys, 1877 (for further supraspecific information see Steiner and Kabat, 2001). The most remarkable character of the genus is a unique, deep and irregular apical fissure at the dorsal side of shell not present among other Scaphopoda (Chistikov, 1982; Scarabino, 1995). Since Chistikov (1952), this genus has been considered as monospecific and restricted to the Atlantic Ocean. During the revision of material from several expeditions carried out by the Muséum national d'Histoire

naturelle, Paris, in the northeastern and southwestern Atlantic Ocean (Brazil) as well as off Solomon Islands in the Pacific, a number of specimens corresponding to the genus were identified. In a preliminary sorting, Brazilian specimens were placed under *H. subterfissus*, but the unexpected finding of representatives in the tropical Pacific, decided us to undertake the present revision. Here, we propose the lectotype of *Heteroschismoides subterfissus* and describe two new species, extending considerably the geographical distribution range of the genus.

MATERIALS AND METHODS

The material was collected during several expeditions carried out by the MNHN and IFREMER, known as BIOGAS I to XII (1972–1981), THALASSA (1970–73) and INCAL (1973): in the Gulf of Gascony; ABYPLAINE (1982): off Portugal and Spain; NORATLANTE (1969): large coverage of the North Atlantic; BIAÇORES (1971): off Azores; BIOVEMA (1977): VEMA Trench; MD55 (1987): Southeastern Brazil; and SALOMON 2 (2004): off Solomon islands.

In view to better define the species, a morphometric analysis was attempted based on selected undamaged shells of the three species. Shell measurements were taken according to Shimek (1989), Steiner (1999) and Steiner and Linse (2000), including length (L); maximum diameter (Max), that is in this case equal to the anterior aperture diameter; maximum curvature (Arc); distance of point of maximum curvature from the apex (Lare); apical aperture diameter (Apd). Besides those measurements, we also estimated the extension of the apical fissure (Fiss) located at dorsal side of shell. To assure independence among variables, we performed a preliminary correlation analysis among all variables with strongly correlated variables (r > 0.70) being excluded. The nonparametric Kruskal-Wallis test was employed to examine for differences of each morphometric parameter (untransformed data) between species. Dunn's multiple comparisons test was used a posteriori to assess signifi cant differences between species. A multivariate approach

was carried out utilizing Discriminant Function (DF) Analysis to integrate all morphometric data in a single analysis. To perform this analysis, we standardized the morphometric data following Romesburg (1984).

Institutional abbreviations used in the text are: BMNH: The Natural History Museum, London; IFREMER: Institut Français de Recherche pour l'Exploitation de la Mer; MNRJ: Museu Nacional, Rio de Janeiro, Brazil; MNHN: Muséum national d'Histoire Naturelle, Paris; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. Other abbreviations are: CP: beam trawl; DC: "Charcot" dredge; stn: station; lv: live-collected; dd: shell only.

SYSTEMATICS

Order Gadilida Starobogatov, 1982 Suborder Entalimorpha Steiner, 1992 Family Entalinidae Chistikov, 1979 Subfamily Heteroschismoidinae Chistikov, 1982 Genus *Heteroschismoides* Ludbrook, 1960

Type Species: *Dentalium subterfissum* Jeffreys, 1877 (by original designation). Recent, northeastern Atlantic Ocean.

Description (Modified from Scarabino, 1995: 302): Shell up to 20 mm length, slightly curved, regularly tapering. Translucent grev when the animal is alive, opaque to polished white or cream when empty. Longitudinally sculptured by 9-10 primary ribs that reach the anterior aperture or vanish towards it. Intercostals spaces convex or straight, smooth or finely striated longitudinally by 8 to 14 lines. Secondary ribs, predominantly a single one, can be present in each intercostal space. Apex with a long and wide irregular fissure on dorsal side early observed in late embryonic stages and juvenile shells. Section polygonal, more notorious at the central zone of shell, fading or not towards the slightly laterally compressed thin oral aperture in adult specimens. Shell fractures and repairs are frequently observed, as well as twisting of shell.

RADULA: Rachidian tooth with anterior margin rounded and lateral margins thick; laterals with sharp pointed primary cusps and 4 important denticles; marginal slightly curved with conspicuous lateral processes, better observed in light microscope.

Distribution: Recent, Atlantic Ocean and tropical Pacific Ocean, bathyal-abyssal.

Remarks: Scarabino (1995: 302) mentioned by mistake "10–12 primary ribs"; in the light of new information this number is here corrected as 9 to 10 primary ribs. Molecular data of *H. subterfissus* has been published by Steiner and Drever (2003).

Heteroschismoides subterfissus (Jeffreys, 1877) (Figures I–6, 15)

Dentalium subterfissum Jeffreys, 1877: 154; t883: 660, pl. 49, fig. 3; Watson, 1879: 516; t886: 10, pl. 1, fig. 10; Pilsbry and Sharp, 1897: 61, pl. 7, figs. 15–19; Warén 1980: 53. Dentalium (Heteroschisma) subterfissum: Henderson, 1920: 58. Dentalium (Dentalium) subterfissum: Nicklès 1979: 47, fig. 5a b. Heteroschismoides subterfissus: Chistikov, 1982: 675, figs. 3, 5;

Steiner 1995: 78; Steiner and Kabat, 2001: 446; 2004: 651.

Description: Shell up to 9.2 mm length, slightly curved, regularly tapering. Translucent shiny grey, presenting fractures and repairs. Longitudinal sculpture of nine primary notorious ribs and a single secondary one in between, more notorious in the dorsal half, all reaching the thin oral aperture. Intercostals spaces convex, finely striated longitudinally by eight lines. Apex with a 2.3 mm long, wide, irregular fissure on dorsal side. Transversal section polygonal, slightly compressed laterally, less apparent at apex.

Type Material: Lectotype, here selected (see remarks), the kargest (9.2 mm) of the three specimens of lot USNM 175018, Ireland, 54°19' N,11°50' W, 1180 fms [2158 m] (Porcupine 1869 stn 16); other paralectotypes: USNM 175017, Off West coast of Ireland, (Porcupine 1869 stn 19a), 2 specimens; USNM 175019, Greenland, 56°11'N 37°41'W, 1450 fms [2646 m], Valorous stn 12, 1 specimen; USNM 175020, 55°40'N 12°46'W, 1476 fms [2694 m], Porcupine 1869 stn 21, 3 specimens; off Azores, Challenger Expedition stn 78, 37°26' N 25°13' W, Azores, 1000 fathoms [1825 m], 7 specimens and 3 fragments, BMNH 1887.2.9.36–40. Two other paralectotypes from Porcupine expedition are deposited at BMNH under code 1885.11.5.1393–4, with a mention "further syntypes in USNM 175017-020".

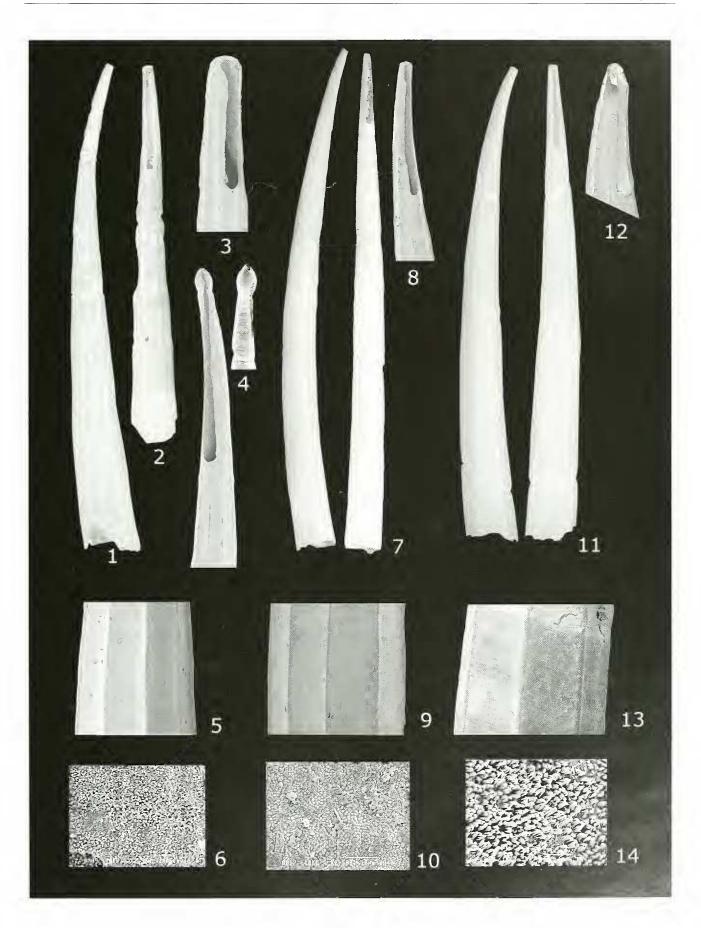
The fact of the species has been partially described on the base of a young specimen (see Remarks) and that the specimen illustrated was not found in the collections revised, lead us to designate the lectotype based on an adult shell.

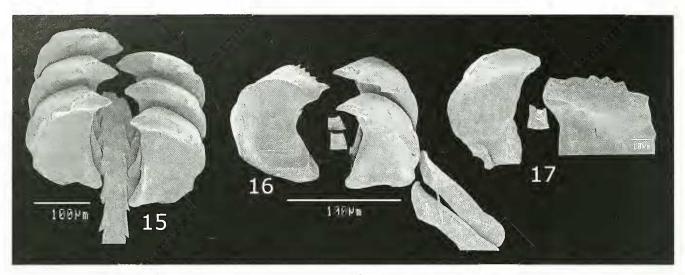
Measurements of Lectotype (mm): Length 9.20, oral aperture 1.00, apex 0.12, are 0.42 at 1.9 from apex.

Type Locality: West of Ireland, 54°19'N, 11°50'W, 1489 m. Porcupine 1869, stn 16 (here selected).

Other Material Examined: Off Gabon (Africa), 2°32′ S, S°18′ E, stn DS20, 2514 m (1 dd); Gulf of Guinea, 4°40′N, 5°39′2E); stn DS30, 3109 m (8 dd) (both WALDA Expedition, CNEXO, Nicklès, 1979), all MNHN.

Figures 1–14. *Heteroschismoides* species. t–6. *H. subterfissus* (Jeffreys, 1977). 1. Lectotype USNM 175018, 9.2 mm. 2. Paralectotype. 3. Detail of the apical fissure. 4. Specimens showing embryonic shell. 5. Detail of longitudinal ribs. 6. Detail of microsculpture on the outer surface of intercostals space. 7–10. *H. maridionalis* new species. 7. Holotype, MNHN, 14 mm. 8. Paratype, detail of apex. 9. Detail of sculpture. 10. Detail of microsculpture on the outer surface of intercostals space. 11–14. *Heteroschismoides antipodes* new species. 11. holotype, MNHN, 9.95 mm. 12. Detail of apex. 13. Detail of sculpture. 14. Detail of microsculpture on the outer surface of intercostal space.





Figures 15–17. Radulae of *Heteroschismoides* species. 15. *H. subterfissus*, rachidian and lateral teeth, internal view. 16. *H. antipodes* new species, external view of lateral tooth (left), rachidian, lateral, and marginal teeth (right), in internal view. 17. *H. meridionalis* new species: rachidian and lateral teeth, internal view.

New Records: Central Atlantic Ocean: Azores Islands: BIAÇORES 1971: stn DS 54, 38°12' N, 28°15' W, 1810 m, 2 dd, stn DS 165, 37°33' N, 25°58' W, 2085–2050 m, 1 dd, DS 173, 37°57' N, 26°08' W, 3225 m, I dd; NORAT-LANTE 1969: stn 02, 53°55′ N, 17°52′ W, 2456 - 2420, 3 lv; stn 84, 36°21' N, 08°43' W, 2871–2875 m, 3 lv, 3 dd; stn 85, 36°25' N, 08°4S', 2573-2580 m, 2 lv, 3 dd; THALASSA 1971, Stn X 336, 44°11' N,05°10' W, 1850-2050 m, I lv, I dd; Eastern Atlantic Ocean: INCAL 1976: stn. DS 01, 57°59' N, 10°40' W, 2091 m, 56 lv, 7 dd; stn. DS 02, 57°59' N, 10°49' W, 2081 m, 51 lv, 3 dd; stn. DS 05, 56°28' N, 11°12' W, 2503 m, 24 lv, 7 dd; stn. DS 07, 55°01' N, 12°31' W, 2884 m, 4 lv, 1 dd; stn. DS 07, 56°27' N, 11°11' W, 2884 m, 5 k, 1 dd; stn. DS 08, 55°02' N, 12°35' W, 2891-2884 m, 3 lv, 2 dd; stn. DS 09, 55°08′ N, 12°53′ W, 2897 m, 2 lv, 2 dd; stn. CP 01, 57°58' N, 10°55' W, 2040-2068 m, 12 ly; stn. CP 02, 57°58' N, 10°42' W, 2091 m, 2 dd; stn. CP 03, 56°38' N,

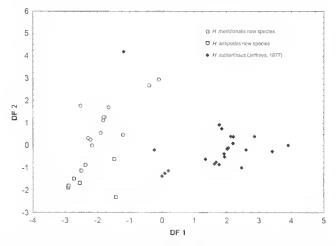


Figure 18. Discriminant function analysis of shell morphometric parameters of *Heteroschismoides* species.

11°06′ W, 2466 m, 3 lv, 1 dd; stn CP 04, 56°33′ N, 11°11′ W, 2438–2513 m, 7 lv, 7 dd; stn CP 05, 56°00' N, 12°29' W, 2884 m, I dd; stn CP 06, 55°02.3' N, 12°40' W, 2888–2893 m, 3 lv, 1 dd; stn CP 07, 55°03' N, 12°46' W, 2895-2897 m, I dd; stn CP 09, 50°15' N, 13°16' W, 2659-2691 m, 2 lv; stn WS 01, 50°19' N, 13°08' W, 2550-2539 m, 5 lv; stn WS 02, 50°19' N, 12°55' W, 2498-2505 m, 1 lv; stn WS 03, 48°19' N, 15°23' W, 4829 m, 2 dd; stn WS 09, 47°28.8 N-47°27.9' N, 09°34' W, 4277 m, 1 dd.; stn OS 0I, 54°14' N, 13°11' W, 2634 m, I lv; BIOGAS II: stn DS 32, 47°32' N, 08°05' W, 2138 m, 3 lv, 3 dd; BIOGAS III: stn DS 37, 47°32' N, 08°35' W, 2110 m, 2 dd; BIOGAS IV; stn DS 52, 44°06' N, 04°22' W. 2006 m, 2 dd; stn DS 51, 44°11' N, 04°15' W, 2430 m, I lv; stn DS 58, 47°34' N, 09°08' W, 2775 m, 3 dd; stn DS 62, 47°33' N, 08°40' W, 2175m, 1 dd; stn DS 64, 47°29' N, 08°35' W, 2156m, 4 lv, 1 dd; BIOGAS V: stn CP 07, 44°09.8' N, 04°16.4' W, 2170 m, 5 dd; BIOGAS VI: stn DS 61, 47°34.7' N, 08°38.8' W, 2250 m, 1 lv, 1 dd; stn DS 62, 47°33' N, 08°40' W, 2175 m, 1 dd; stn DS 63, 47°33' N, 08°35' W, 2126 m, 1 lv; stn CP 08, 47°03' N, 08°39' W, 2177 m, 2 lv, 1 dd; stn CP 09, 47°33' N, 08°44' W, 2171 m, 1 lv; stn CP 24, 44°08' N, 04°16' W, 1995 m, 3 dd; stn DS 71, 47°34' N, 08°34' W, 2194 m, 3 lv, 5 dd; stn DS 86, 44°04.8' N, 04°18.7' W, 1950 m, 1 dd; stn DS 87, 44°05' N, 04°19' W, 1913 m, 3 ly; BIOGAS VII: stn CP 26, 47°33' N, 08°34' W, 2115 m, 1 lv; BIOGAS VIII: stn KG 145, 47°33' N, 08°39' W, 2170 m, 1 dd; stn KG 147, 47°33.40' N, 08°40.70' W, 2190 m, lv, dd; stn KG 149, 47°33' N, 08°39' W, 2165 m, 1 dd; stn KC 151, 47°34' N, 08°39' W, 2205 m, 1 ly; BIOGAS IX: stn CP 34, 47°32' N, 08°25' W, 1970 m, 1 dd; BIOGAS XI: stn CP 37, 47°34' N, 08°41′ W, 2175 m, 2 ly,

Distribution: Eastern Atlantic Ocean: Greenland, off West Ireland, Gulf of Gascony, off Spain and Portugal to Gulf of Guinea, West Africa (Jeffreys, 1877; Watson, 1879, 1886, Locard, 1898; Nicklès, 1979). Alive in 940– 2987 m, shells down to 4829 m (present paper). Richest depth for live material: 2040–2503 m (present paper).

Remarks: Jeffreys partially described the species based on a juvenile specimen, since he mentioned "... posterior end bulbous" and illustrated this morphology in plate 49, fig. 3. flowever, no juvenile specimen was detected among the type material. In addition, he wrote that the slit is in the "under or ventral side", which in fact corresponds to the dorsal side in normal position of the animal. Jeffreys also mentioned the presence of 12 to 16 ribs, but we did not find any specimens with that number of ribs. However, it is possible that secondary ribs and intercostal striae might have been, in part, counted inappropriately for the original description. To clarify, in the description we enumerated only the primary ribs because the number of secondary ribs varies with age and among specimens but the number primary ribs is constant among specimens and through the life of the specimen. Specimens with embryonic shell are often observed.

Heteroschismoides subterfissus was also mentioned in the CHALLENGER expedition from "stn 120 - 8°37′ S 34°28′ W, Pernambuco, South America 675 fathoms [1232 m] red mud" (Watson, 1SS6). The lot in which this reference was based was not located in BMNH collections by the senior author. In the distribution paragraph, Watson (18S6) wrote "Habitat.- Davis Strait. 1785 fathoms. North Atlantic; various Stations off the West Coast of Ireland. 1180 to 1476 fathoms (Jeff.)." He did not mention Pernambuco.

The material from Pernambuco may belong to the new species described below or, as suggested by Henderson (1920: 58), could also correspond to specimens of *Pertusiconcha callithrix* (Dall, 1889), since young specimens of this species, specially those with a broken apex, can easily be misidentified as species of *Heteroschismoides* (Scarabino, pers. observ).

Heteroschismoides meridionalis new species (Figures 7–10, 17)

Description: Shell 14 mm length, slightly curved, regularly tapering, opaque white. Longitudinal sculpture composed of nine rounded-edge primary ribs, all reaching but fading towards the oral aperture. No secondary ribs. Intercostal spaces concave in posterior three quarters and straight to convex at the anterior fifth, presenting 12 very faint, fine striae throughout. Apex with a 2 mm long, wide irregular fissure on dorsal side. Crosssection polygonal, less angular at apex and at the slightly laterally compressed anterior aperture.

Measurements of the Holotype (mm): Length 14.0, oral aperture 1.0, apex 0.1, arc 0.8 at 6.7 from apex.

Type Material: Holotype (lv) MNHN 20902 and 14 paratypes (dd), 13 MNHN 20903–20906, 1 MNRJ 12707.

Type Locality: Off Espírito Santo, Brazil, 18°59.1′ S, 37°47.5′ W, 1540–1550 m [MD 55 stn DC 70].

Material Examined: Southwestern Atlantic Ocean: MD 55 stn CP 68, 18°55.6' S, 37°49.1' W, 1200–1500 m, 1 dd (paratype MNHN 20903); stn DC 70, 18°59.1' S, 37°47'8 W, 1540–1550 m, 1 k (holotype MNHN 20902), 26 dd (7 paratypes MNHN 20904, 1 paratype MNRJ 12707); stn DC 72, 19°00.4' S, 37°48.8' W, 950–1050 m, 4 dd (paratypes MNHN 20905); stn CB 77, 19°40.6' S, 37°48.1' W, 790–940 m, 9 dd (2 paratypes MNHN 20906); stn. CB 79, 19°01.8' S, 37°47.8' W, 1500–1575 m, 10 dd; stn CB 106, 23°54.2' S, 42°10.5' W, 830 m, 15 dd; stn. CB 107, 24°00.3' S, 42°14.4' W, 1020 m, 11 dd.

Etymology: *Meridionalis*: Southern. Name refers to the taxon's distribution in the Southern Hemisphere.

Distribution: Brazil: Espírito Santo and São Paulo. Alive in 1540 m, shells in 790–1540 m depth.

Heteroschismoides antipodes new species (Figures 11–14, 16)

Description: Shell to 9.95 mm length, slightly curved at the apex, regularly tapering. Opaque white. Longitudinal sculpture of ten primary ribs, all reaching the oral aperture. Intercostal spaces concave and smooth. Apex with a wide irregular fissure 1.7 mm long on dorsal side. Cross section polygonal, less obvious at apex, slightly laterally compressed at the anterior aperture.

Measurements of Holotype (mm): Length 9.95, oral aperture 0.9, apex, 0.1, arc 0.4 at 2.76 from apex.

Type Material: Holotype (dd) MNHN 20907 and 10 paratypes (7 lv, 3 dd) MNHN 20908–20910

Type Locality: Solomon Islands, 07°49.3′ S, 157°41.2′ E, 1045–1118 m [SALOMON 2 Stn. CP2217].

Material Examined: Solomon Islands. SALOMON 2: stn CP2182, 08°47.0' S, 157°37.9' E, 762–1060 m, 16 dd; stn CP2197, 08°24.4' S, 159°22.5' E, 897–1057 m, 2 lv, 2 dd (3 paratypes MNHN 20909); stn CP2217, 07°49.3' S, 157°41.2' E, 1045–1118 m, 1 lv, 3 dd (holotype MNHN 20907 and 3 paratypes MNHN 20908), stn CP2218, 07°56.3' S, 157°34.6' E, 582–864 m, 4 lv (paratypes MNHN 20910) 14 dd; stn CP2253, 7°26.5' S, 156°15.0' E, 1200–1218 m, 10 dd.

Etymology: From Greek *antipodcs*, meaning those living on diametrally opposed places on Earth.

Distribution: Solomon Islands, alive in 1200 m; shells 762–1200 m depth.

MORPHOMETRIC RESULTS AND DISCUSSION

Table 1 lists the mean, standard deviation, minimum, and maximum values for each morphometric parameter for the three species. Significant differences in all morphometric parameters were observed between the species (Kruskal-Wallis test; p < 0.01), except for the maximum curvature (Arc). This univariate comparison showed that *H. meridionalis* new species and *H. subter*-

	II. meridionalis (n=12)		H. antipodes (n=8)		H. subterfissus (n=23)			
	mean (±SD)	min–max	mean (±SD)	mi <mark>n-</mark> max	mean (±SD)	min–max	KW	Dunn's test
L	13.3 (1.6)	11.1–16.5	8.9 (0.8)	7.9–10.7	14.2 (2.6)	10.0-19.0	19.19°	st sb an
Max	1.0(0.05)	0.9 - 1.1	1.0 (0.07)	1.0 - 1.2	1.4 (0.16)	1.0 - 1.7	29.76°	st an sb
Are	0.5(0.4)	0.1 - 1.2	0.5(0.1)	0.4-0.7	0.5 (0.1)	0,2-1.0	0.82 ns	st sb an
Lare	6.1 (0.8)	4.8-7.2	3.5 (0.6)	2.1 - 4.0	5.4 (2.5)	2.2 - I1.4	14.98°	st sb an I───I I──
Apd	0. <mark>1 (0.05</mark>)	0.1 - 0.2	0.2 (0.00)	0.2-0.2	0. <mark>2 (</mark> 0.05)	0.2-0.3	20.15°	st an sb
Fiss	2.1 (0.5)	1.5 - 3.1	1.4 (0.2)	1.1 - 1.5	1.9(0.5)	1.2-3.0	13.32°	st sb an ⊢−−1 ⊢−

Table 1. Shell morphometric parameters with minimum (min), maximum (max), mean values and standard deviation (\pm SD) for thethree new species of *Heteroschismoides*. L: length; Max: maximum diameter (= anterior aperture diameter); Arc: maximum curvature;Lare: distance of point of maximum curvature from the apex: Apd, apical aperture diameter; Fiss: fissure length. KW: Kruskal-Wallistest); ns: not significant; °p<0.001. The horizontal lines at Dunn's test represents absence of statistical differences.</td>

fissus are more similar, differing significantly only in maximum diameter (Max) and apical aperture diameter (Apd) (Table 1). *Heteroschismoides meridionalis* new species is also less shiny and the intercostal spaces are more densely striated: 12–15 striae (observed on stained or coated specimens due to the difficulty to be observed without any treatment) against 8–10 in *H. subterfissus* (well observed under lens) (these data was obtained from counting 10 specimens of each species).

Individuals of *Heteroschismoides antipodes* new species are significantly smaller than individuals of the other two species for both shell length and fissure extension. The distance of point of maximum curvature from apex (Larc) in *H. antipodes* new species specimens is located nearer to apex than in specimens of both *H. meridionalis* new species and *H. subterfissus* (Table 1). In addition, *H. antipodes* specimens are opaque, due to their coarsest surface microsculpture. Specimens of this species have smooth intercostal spaces without secondary ribs and striae, and the primary ribs are more apparent.

The multivariate discriminant function analysis was able to distinguish three groups among the specimens we examined that correspond to three species (Wilks' Lambda = 0.12; $F_{6,76} = 24.27$; p < 0.0000). This analysis classifies about 97% of the cases correctly (only 1 out of 43 specimens were incorrectly classified) (Figure 3). The model was constructed with 3 parameters (Max, L : Max, Larc). The variable L, which was highly correlated with Lare (r = 0.80) and Fiss (r = 0.74), was excluded. The Discriminant Functions (DF) based on the raw coefficients of canonical variables are shown below:

DF1 = 2.5439Max + 1.0378L : Max - 0.7366Larc

DF2 = 0.7249Max + 2.1404L : Max - 0.8328Lare

The radulae of the three species, here illustrated, are quite similar and further studies would be necessary to test the existence of interspecific differences, as it is the case in most Scaphopoda. Finally, the findings of *Heteroschismoides* in the Solomon Islands show the genus to have worldwide distributed instead of being confined to the eastern Atlantic Ocean. However, better sampling of areas of the Indian Ocean (one of the less known tropical areas for scaphopod diversity) could eventually confirm whether the genus is also represented in that ocean.

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